

ON THE ADULT AND JUVENILE STAGES OF *VANBENEDENIA CHIMAERAE*
(HEEGAARD, 1962) (COPEPODA: LERNAEPODIDAE) FROM
AUSTRALIAN WATERS.

By Z. KABATA, Marine Laboratory, Aberdeen.

(Communicated by Dr. J. C. Yaldwyn.)

(Forty Text-figures.)

[Read 29th July, 1964.]

INTRODUCTION.

In his interesting paper on the parasitic Copepoda from Australian waters, Heegaard (1962) described a lernaepodid species, which he assigned to the genus *Tracheliastes* Nordmann, 1832, and to which he gave the name *T. chimaerae*. Heegaard's generic diagnosis was influenced by Wilson's (1915) description of *T. grandis*. It had been suspected, however (Monod and Vladykov, 1931), and eventually proved (Kabata and Bowman, 1961) that Wilson was at fault in this instance and that this species should have been placed in the genus *Vanbenedenia* Malmgren, 1860. The same is true of Heegaard's Australian species. The present author, with the knowledge and consent of the discoverer, proposes, therefore, to re-name it *Vanbenedenia chimaerae* (Heegaard, 1962).

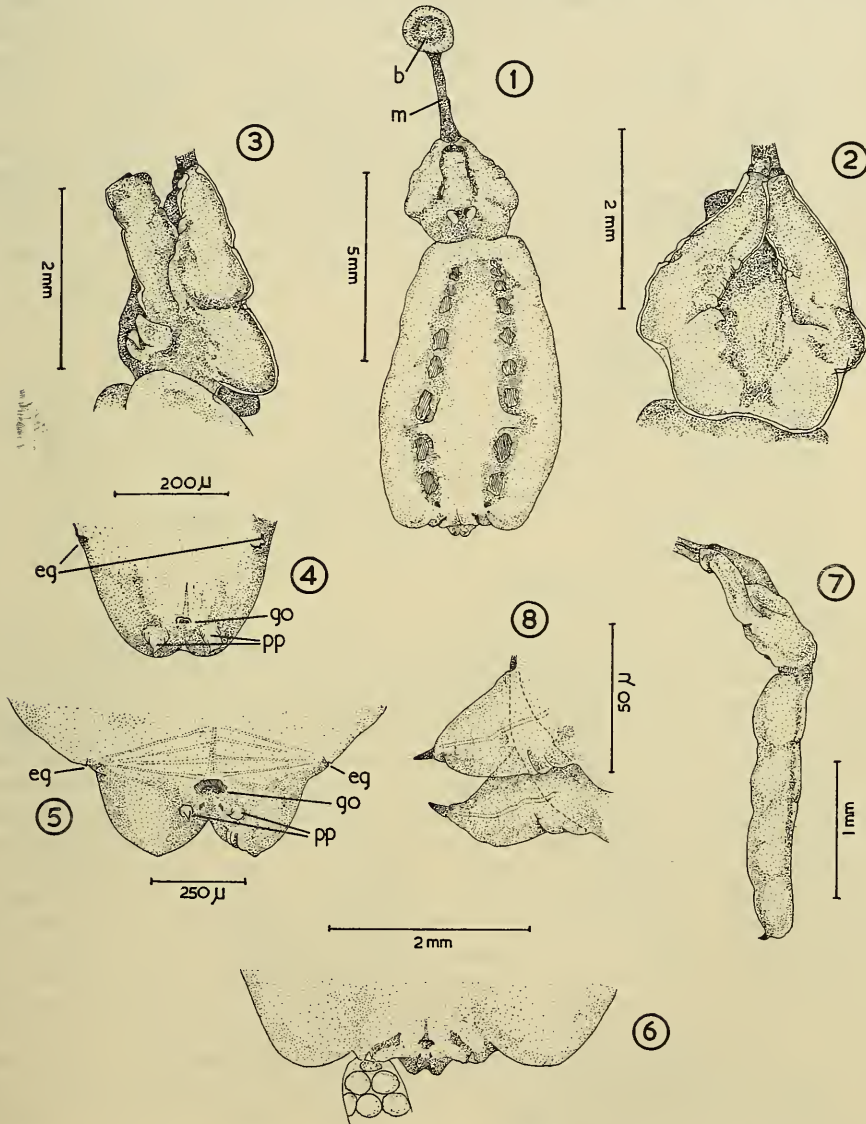
Tracheliastes and *Vanbenedenia* differ from each other in several important respects. Thus, to mention only two, the position of the cephalothorax in *Tracheliastes* (as suggested by the name) is dorsal to the main axis of the trunk, while the opposite obtains in *Vanbenedenia*; *Tracheliastes* parasitizes freshwater fishes of the Palaearctic Region, while the only known host of the genus *Vanbenedenia* is *Chimaera*, a deep-sea holocephalan genus with world-wide distribution.

The author's earlier work on the genus *Vanbenedenia* (cf. Kabata, 1958, 1959) suggested that the biology of this genus, as well as some of its morphological features, are of considerable interest to the student of Lernaepodidae. To explore these features further, the author studied, as a loan from the Australian Museum, the specimens of *V. chimaerae* which constituted a part of Heegaard's original material. The specimens included adult females, juvenile females and larval individuals at the stage of development which is variously referred to as "pupa" or "chalimus". They were examined, both entire and dissected for the better study of the appendages, under magnifications up to $\times 900$, with the aid of the phase-contrast illumination. The dissections were carried out in Berlese's fluid, which was also used as the mounting medium. No stains were employed. Each appendage was observed from as many aspects as possible, before final drawings were made. The illustrations shown below are all free-hand drawings, made with the aid of an eyepiece graticule.

DESCRIPTION OF THE ADULT FEMALE.

General appearance (Figs 1-3, 6). The body of the adult female is easily divided into the cephalothorax and the trunk. The cephalothorax is cylindrical and fairly short, forming with the "arms" (the first maxillipeds) a broad shoulder region, separated from the trunk by a distinct waist-like groove (Fig. 1). It is ventrally inclined to the main axis of the trunk, the arms fusing above it and preventing its dorsal movements (Figs 2-3). The trunk is longer than broad (length : width ratio about 1.5 : 1) in the adult ovigerous females. The greatest width of the trunk is usually about $\frac{2}{3}$ from the anterior end of the trunk. The trunk is flattened dorso-ventrally, the outer margins in the preserved specimens being more swollen than the area

immediately adjacent to them. At some distance from the lateral margins of the trunk a row of depressions extends almost along the entire length. These depressions (Fig. 1), which are about 10 in each row, are made by heavily sclerotized plaques and serve as the points of insertion for the dorso-ventral musculature of the trunk. The posterior end of the trunk is truncated, its exact shape and structure depending on the age of the female. In the youngest adult specimen available for examination (Fig. 7) and already attached to the host by means of the bulla, the end of the trunk appeared as



Figs 1-8.—1. Adult female, ventral. 2. Adult female, cephalothorax, dorsal. 3. Adult female, cephalothorax, lateral. 4. Young female, posterior end of the trunk, ventral. 5. Young female, older than in Fig. 4; posterior end of the trunk, ventral. 6. Adult female, posterior end of the trunk, ventral. 7. Young female, entire, lateral. 8. Posterior processes of specimen shown in Fig. 7, lateral.

Lettering on figures.

b, bulla; *ch*, central canal of manubrium; *eg*, point of attachment of egg-strings (oviduct opening); *en*, endopod; *ex*, exopod; *go*, genital orifice; *m*, manubrium; *pp*, posterior processes (caudal furca); *t*, ventral tubercle of 2nd mxp; *x*, *y*, *z*, elements of cephalic armature.

shown in Figure 4. The trunk of this specimen was 2.17 mm. long. The posterior processes (derived from the caudal furca of the juvenile stages), the genital orifice and the future points of attachment for the egg-strings can be seen in this specimen. Posterior processes are shown enlarged in Figure 8. With increasing age, the latero-posterior margins begin to swell out laterally and in a specimen with the trunk 3.13 mm. long the end of the trunk appears as shown in Figure 5. The swelling begins at the level of the oviduct openings (points of attachment of the egg-strings). The definitive shape of the extremity of the trunk, as seen in an ovigerous female with the trunk 6.44 mm. long, is shown in Figure 6. The lateral swelling has now progressed to the point at which the appearance of the end of the trunk becomes greatly modified. The relative sizes of the posterior processes in Figures 4, 5 and 6 give a good illustration to the changes, with age, of this part of the trunk.

Some idea of the dimensions of the adult females is given by the figures below. It must be remembered that the measurements (in mm.) were taken from specimens preserved for many years in alcohol and with cephalothoraces at different degrees of contraction. The data concerning this part of the body must, therefore, be taken as very general in character. The measurements are based on 12 female specimens.

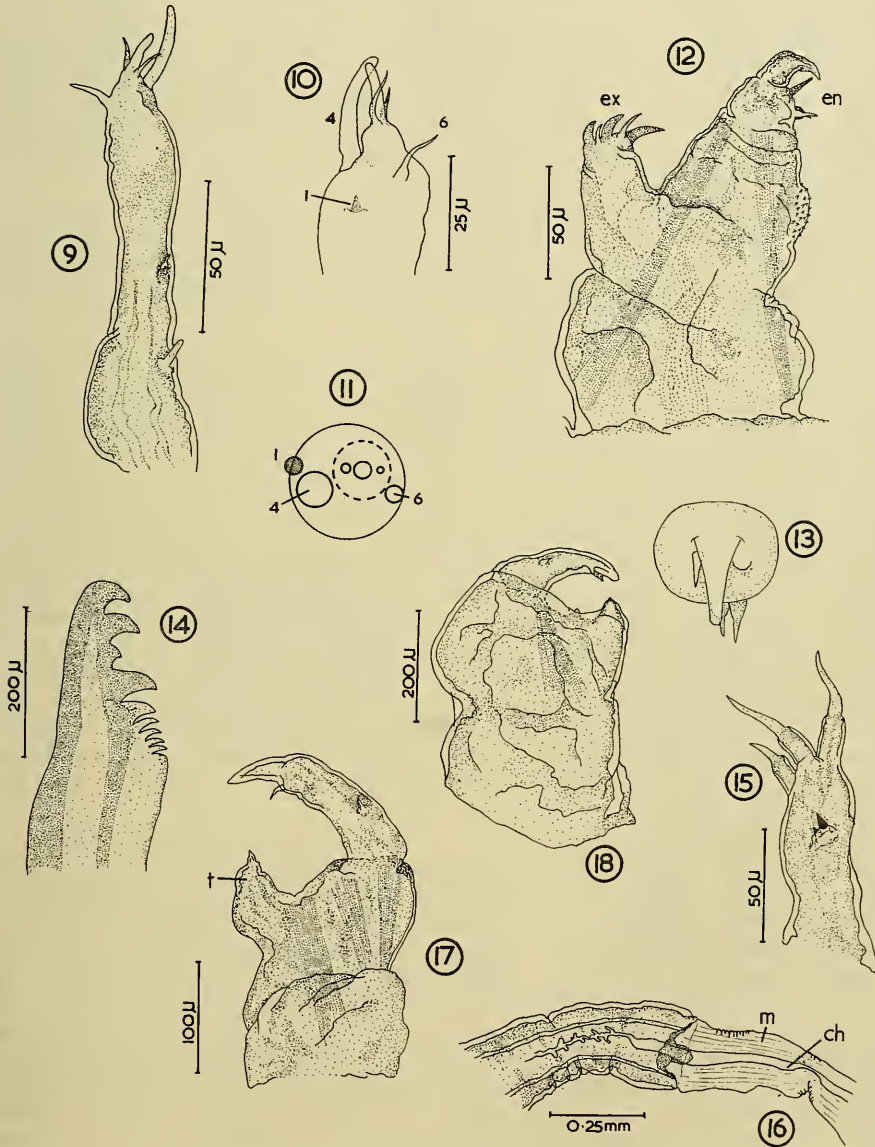
		Range	Mean
Cephalothorax length	2.2-2.8	2.4
„ „ width	0.6-0.7	0.7
Shoulder region, width	2.2-2.6	2.4
Trunk length	5.4-7.2	6.4
„ width	2.7-4.8	4.0
Arms, length	1.3-2.2	1.8
„ „ diameter at the base	0.6-0.9	0.8
Egg-strings length	6.2-9.4	7.8
„ diameter	0.7-0.8	0.8
Eggs, diameter (approximate)	0.2-0.3	0.3

Appendages.

The first antenna (Figs 9-11). Even in the smallest specimens, already attached by the bulla and, therefore, considered as adult, no true segmentation of the first antenna has been observed by the author. In some specimens, however, transverse wrinkles in the cuticle resemble segmental divisions. The base of the appendage (Fig. 9) is somewhat inflated and bears on its dorso-median aspect the usual lernaeopodid spine. It is possible that the spine shown in Figure 9 has been broken and is shorter than it should be. The central part of the antenna is more slender. It also carries on its dorso-median aspect a short spine, found in this position in some other genera of Lernaeopodidae. Towards its apex, the antenna dilates again in the manner typical for the genus *Vanbenedenia*. The apical armament of the first antenna is shown in detail in Figures 10 and 11. Near to the centre of the apex is a prominent swelling, shown in Figure 11 as a dotted circle. It is tipped by three spines, one central, strong and with a blunt, finger-like end, and two others on its both sides. The inner aspect of the tip is occupied by a strong and also blunt-ending spine, which can be seen as the homologue of the similar spines in all the other lernaeopodid genera studied by the author (Kabata, 1963, 1964, 1964a, 1964b) and labelled (4). The dorso-lateral aspect carries a slender, whip-like spine labelled (6) and also homologous with similar spines in other Lernaeopodidae. A small spine (marked 1 in Figs 10 and 11) is present near the base of spine (4).

The second antenna (Figs 12 and 13) resembles the corresponding appendages of most of the lower Lernaeopodidae. An indistinctly segmented sympod (consisting of either one or two segments) carries distally a two-segmented endopod and a one-segmented exopod. The proximal segment of the endopod (Fig. 12, *en*) has a spinulated pad on its ventral margin. Its distal segment is armed with a hook and several accessory spines, shown diagrammatically in Figure 13. One slender spine is located on

the ventro-median aspect of the base of the central hook and points obliquely upwards. Ventral to the base of the hook and at some distance from it are two structures, situated side by side. The lateral one is a sharp-pointed spine with slightly inflated base, while the medial one is relatively broader at the base and shorter, also ending in a sharp point. An indistinct swelling is present on the ventro-lateral aspect of the base of the central hook. In all its essential aspects, this armature resembles that of the second antenna of *V. kroyeri* (cf. Kabata and Bowman, 1961). The exopod (Fig. 12, *ex*) is not dorsal to the endopod, as in most lernaepodid genera, but rather dorso-



Figs 9-18.—9. Adult female, 1st antenna, dorsal. 10. Adult female, tip of 1st antenna, lateral. 11. Diagram of the apical armature of 1st antenna. 12. Adult female, 2nd antenna, lateral. 13. Diagram of the armature of endopod, 2nd antenna. 14. Adult female, distal part of mandible, lateral. 15. Adult female, maxilla, lateral. 16. Young female, distal part of 1st maxilliped and base of manubrium. 17. Young female, 2nd maxilliped, lateral. 18. Adult female, 2nd maxilliped, lateral.

lateral. The study of the position of this segment is made difficult by the great mobility of the tip of the endopod. The dorso-ventral axis of the second antenna is usually considered as being parallel with the long axis of the endopod's central hook. Since the twisting of the endopod changes the position of the hook, the relative positions of the two rami are also apparently altered. It can be accepted, however, that the exopod is not directly dorsal to the endopod. Since this position is one of the diagnostic features of the genus *Vanbenedenia*, it is rather important to know it. The tip of the exopod is armed with three powerful claws, pointing outwards. Between the bases of these claws are two spines, much more slender than the claws themselves and rather shorter.

The mandible (Fig. 14) is a long, blade-like structure, its dentiferous margin armed with a series of nine teeth. The teeth are not uniform in size (mandibular formula H2, Z1, H1, N5). The first two teeth are primary and are followed by a small secondary tooth. This, in turn, is followed by another primary tooth and a series of "Nebenzähne" consisting of five teeth, progressively smaller. The usual cutting blade follows the last tooth of the proximal series.

The maxilla (Fig. 15) is also a typical lernaepodid limb, with stout sympod and the endopod ending in three papillae, arranged dorso-ventrally and ending in stout setae. The ventral of these is the shortest. The exopod is lateral in position and vestigial, consisting of two short, subequal spines, the smaller one being difficult to observe.

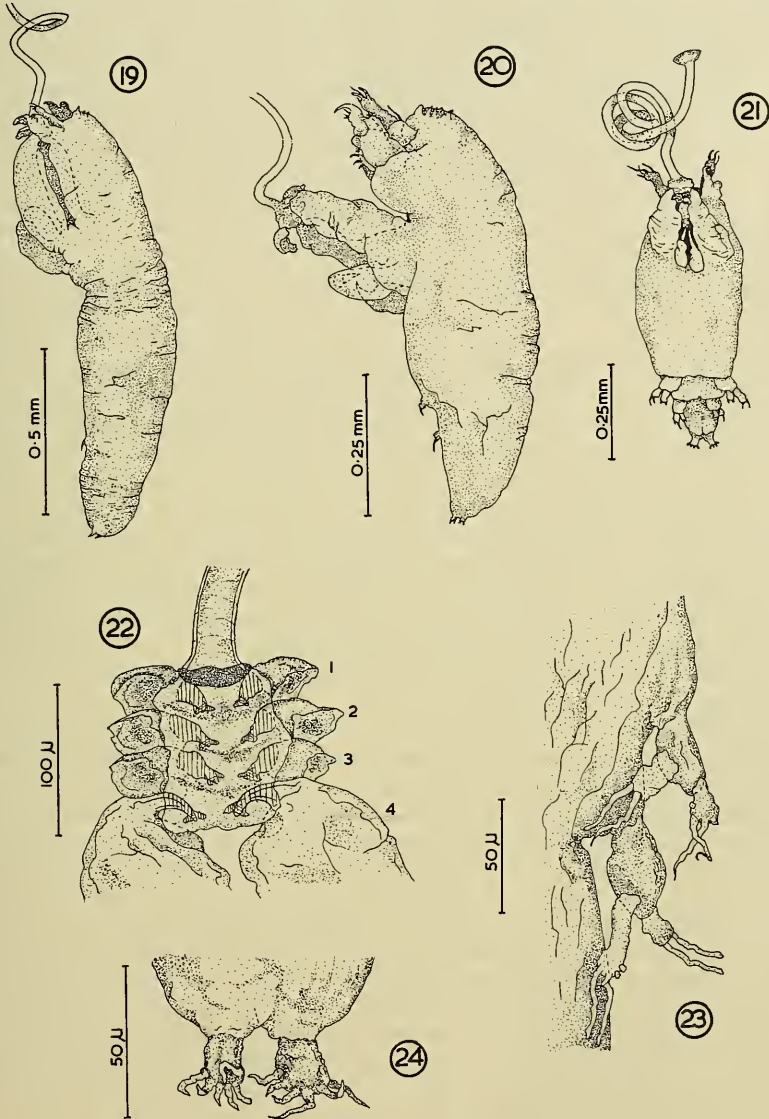
The first maxillipeds (Figs 1-3, 16) are the appendages which form the characteristic "arms". They arise from the cephalothorax near the point where it expands into the shoulder region. In the young adult females, with bulla recently formed, the tips of the arms are close together and fused by means of the manubrium (Figs 1 and 16, *m*), to the formation of which both arms have contributed. The bulla at this stage is still colourless and soft and the anchoring apical swelling (Fig. 1, *b*) is still missing. The manubrium appears like an empty sheath (Fig. 16, *m*) or rather two sheaths fused together, but readily pulled apart. Each half of the double central channel (Fig. 16, *ch*) can be clearly observed. In older specimens (Fig. 1) the bulla becomes sclerotized; it is hard and dark-brown. The two halves can no longer be separated. The manubrium now ends in a roughly lenticular or spherical swelling, formed by the secretion drained through the central channel. The length of the manubrium in the young females is about 1.75 mm., reaching up to 2.5 mm. in the fully mature specimens. The long diameter of the apical swelling of the bulla varies from 1.7 to 1.8 mm. The host which carried the specimens examined was infested by some 50 parasites and, since all of them were found on the claspers, the animals were crowded together. Their bullae were often fused in groups of three, or four, with some degree of distortion.

The second maxilliped (Figs 17 and 18) differs with the age of the female. In the young, recently attached females which carried no egg-strings, the shape of the second maxilliped was as shown in Figure 17. The main body of the limb appears to consist of two segments, though the subdivision is not clear. The apical segment forms a subchela which closes against a prominent tubercle on the ventral margin of the penultimate segment. The tubercle is tipped with a short but fairly strong spine. The tip of the subchela carries a slightly curving claw, with a short auxiliary spine near its base. There is also another short spine on the outer aspect of the subchela, near $\frac{1}{3}$ of its length from the base. All these features are also recognizable in the mature female (Fig. 18), though their relative sizes are much different. The subchela is much smaller, with claw and the other two spines much weaker. The ventral tubercle of the penultimate segment is also relatively smaller, its spine observable only with difficulty.

DESCRIPTION OF THE JUVENILE STAGES.

Of the 14 adult specimens examined by the author, nine had frontal filaments, or parts of filaments, of the juvenile stages attached to their cephalothoraces, mainly arms or second maxillipeds. Six of these specimens had the juveniles still suspended from

the proximal ends of the filaments. Among these developmental forms four stages could be distinguished. The developing parasites were attached to their frontal filaments by means of their first maxillipeds. The terminal claws of these limbs were firmly embedded in the enlarged bases of the filaments. With each succeeding moult another flow of secretion followed, gluing the next stage of the parasite to the end of



Figs 19-24.—19. Chalimus III, lateral. 20. Chalimus II, lateral. 21. Chalimus I, lateral. 22. Chalimus IV, tips of first maxillipeds and base of frontal filaments, showing claws of the preceding moults (numbered). 23. Chalimus I, thoracic legs. 24. Chalimus I, caudal furca, dorsal.

the filament. The cuticle of the preceding stage disintegrated, leaving the tips of the first maxillipeds hanging like empty gloves from the base of the filament (Fig. 22). The largest number of the discarded pairs of cuticular claws was three. The presence of these remains allows one to determine in each case the exact developmental stage of the specimen. Those which have no such empty claw belong obviously to the first

chalimus stage, those with one pair to the second chalimus stage, etc. The oldest specimen examined by the author belonged, therefore, to the chalimus stage IV.

The external examination of these stages of development showed no differences between the future male and female individuals until chalimus stage III, when the female specimens could be distinguished by more elongate "arms".

General appearance (Figs 19-21). The youngest stage examined (i.e., chalimus I) is shown in Figure 21. At this stage of development, the body of the parasite consists of the cephalothorax, free thorax and abdomen, with caudal furca. With the exception of the thoracopods, the appendages already present at this stage persist in the mature parasite. The number of the free thoracic segments is not easy to distinguish. The anterior two can be recognized by the presence of thoracopods, with which they are associated. Only one specimen at this stage was examined by the author. Its total length was 0.68 mm., the cephalothorax length being 0.51 mm. (from the anterior margin of the head to the level of the first pair of thoracopods). The cephalothorax is roughly oval and devoid of dorsal carapace.

No great change takes place in the appearance of the parasite between the chalimus I and chalimus II stages (Fig. 20). Two specimens at the latter stage measured 0.69 and 0.73 mm. respectively, the increase in size being due to the growth of the posterior part of the body (cephalothoraces of both specimens were 0.50 mm. long). There is some elongation of the "arms" and the thoracopods begin to atrophy. This trend in development continues on change to the chalimus III stage (Fig. 19), although the change is accompanied by a more pronounced increase in size. The only specimen of this stage was 1.37 mm. long. The relative increase in the sizes of the cephalothorax and the posterior (trunk) part of the body cannot be determined easily, since only one pair of thoracopods was found by the author in this specimen and the exact limits of the two parts could not be determined. There is little change between the general shape of chalimus III and chalimus IV stages. Two specimens of chalimus IV examined by the author were damaged and could not be measured, but the overall appearance of these specimens differed only little from chalimus III. The only possible difference was the now definitely pronounced elongation of the "arms", already noticeable in chalimus III.

The first antenna (Fig. 25) of the chalimus I shows all the features described for the adult appendage. The state of the specimens made the examination difficult, but it was possible to see that both the general shape of the limb and all the apical armament spines are quite like those of the adult. The main difference between the first antenna of chalimus I and that of the adult is the length of the apical armament spines, which can be seen by referring to Figures 9 and 25. Two unusual features are noticeable in the first antenna of chalimus I. The long spine present on the dorso-median aspect of the basal part of the limb appears to have another small spinule at its base. The two small spines present at the central prominence of the apex (marked ? in Fig. 25) appear to be fused at the bases. These two features, however, were observed in only one antenna, its companion from the opposite side having neither of them. It is, therefore, difficult to say whether the fusion of the two spines was an aberration of structure, or whether the additional spine on the dorso-median aspect of the base is a regular feature. Neither of these features was found in the following stages of development. Beginning with chalimus II, the first antenna differed from that of the adult in size only.

The second antenna (Figs 26-28). At the chalimus stage I, this appendage is already fully formed, showing most of the features present in the adult. Its sympod appears to consist of two segments, the distal one of which bears the endopod and the exopod (Fig. 26, *en*, *ex*). The endopod is two-segmented. The proximal segment is unarmed, the distal segment carries apical armament described for the adult and figured in Figures 12, 13, 26 and 27. Figure 26 shows the hook of the distal segment turning away from the observer, but its true shape can be seen in Figure 27, which shows the distal segment of the endopod of chalimus II in lateral view. The only

difference between the endopod of chalimus I and the succeeding stages is the appearance of the spinulated pad on the proximal segment, beginning with chalimus II. The central hook, which is long and slender in the early stages, becomes progressively shorter and more robust, to assume the adult shape shown in Figure 12. The exopod of the second antenna undergoes more extensive changes with age. In chalimus I, as shown in Figure 26, it is one-segmented and armed with two long setae. In chalimus II three small tubercles appear on the tip of the exopod, one between the bases of the setae and two on both sides of these structures. In chalimus III the tubercles increase in size and acquire sharp points (Fig. 28), while the setae between them become relatively shorter. This trend is further accentuated in chalimus IV. By the time the parasite becomes adult, the three tubercles will have developed into three powerful claws (Fig. 12), completely dwarfing the setae between them.

The mandible (Fig. 29) also undergoes only small changes from chalimus I to the adult parasite. At the earliest stage examined, it already has its definitive shape, differing from the adult only in size and in the absence of the third tooth, the only secondary tooth of the mandible. That tooth first appears at the chalimus III stage. The distal tooth of the mandible is somewhat smaller in chalimus I than in the succeeding developmental stages.

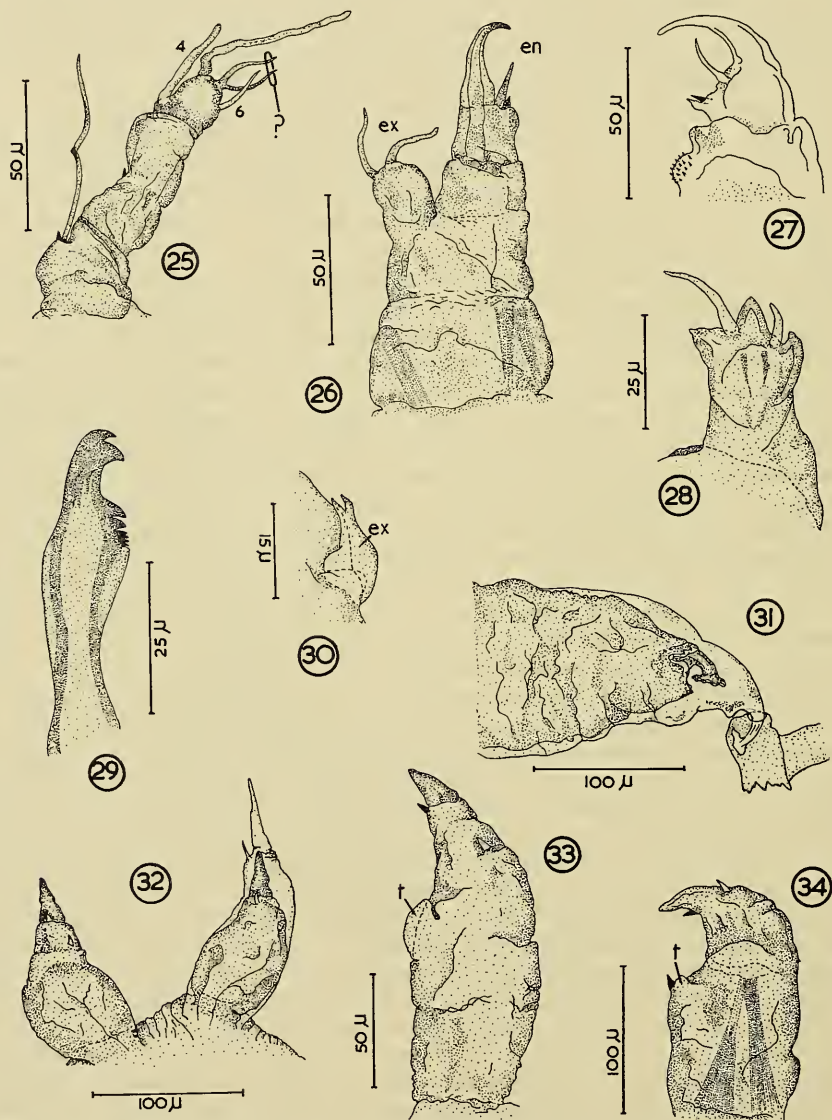
The maxilla (Fig. 30) also shows few changes in the course of its development. The difference between chalimus I and the adult (Fig. 15) is in the larger size of the exopod, which in chalimus I is a definite segment with a bifid tip. It appears to be gradually reduced and survives in the adult only as the two spines, vestiges of the tip.

The first maxilliped (Fig. 31) changes little in the four chalimus stages examined. Figure 31 shows the formation of the appendage of chalimus II within the cuticle of chalimus I. It can be seen that these appendages are quite similar. In both stages they end in curving claws, whose tips are provided with anchor-like extensions used to secure the limb in the base of the frontal filament. Under the cuticle of the preceding stage, the appendage of the next is usually profusely wrinkled, foreshadowing the expansion which is to occur at the moult. This expansion and elongation is the most marked feature of the development of the first maxilliped. By the time the animal reaches the adult stage, the limb is quite long and fused to its neighbour by the manubrium of the bulla. By then the terminal claw disappears, but it is still present in chalimus IV, the oldest pre-adult stage examined by the author (Fig. 22).

The second maxilliped (Figs 32-34, 40) is the appendage which shows most extensive changes in the course of its development, observed in chalimus specimens. The earliest stage is shown in Figure 32, illustrating both second maxillipeds of a chalimus I which is ready to moult. The right member of the pair shows the limb of the next stage, formed within the cuticle of chalimus I. In the course of dissection, this cuticle was pulled off the left member of the pair, showing the limb of the next stage. In chalimus I, then, the second maxilliped is apparently one-segmented, almost cylindrical and ending in an anteriorly-pointing, straight claw, with an auxiliary spine at its base. In chalimus II, the subchela, the second segment of the appendage begins to form and its lateral spine makes its appearance. Figure 33 shows the maxilliped of chalimus III, recently removed from the cuticle of the preceding stage. The subchela is now more distinguishable and the ventral tubercle of the penultimate segment begins to form (Fig. 33, *t*). A fully developed limb of chalimus III is shown in Figure 34. The subchela is now at an angle with the rest of the limb. Both its auxiliary spines and its terminal claw are easily observable. An apical spine has also appeared on the tip of the ventral tubercle. A great change appears to take place between chalimus III and IV, although the author could not determine with absolute certainty the course of development at this point of the parasite's life history. In one of the chalimus IV specimens examined, the second maxilliped did not greatly differ from the corresponding limb in chalimus III, while in the other specimen it seemed to have gone through extensive changes. The latter specimen, however, was badly preserved and it is possible that parts of its cuticle had been sloughed off, exposing structures properly belonging

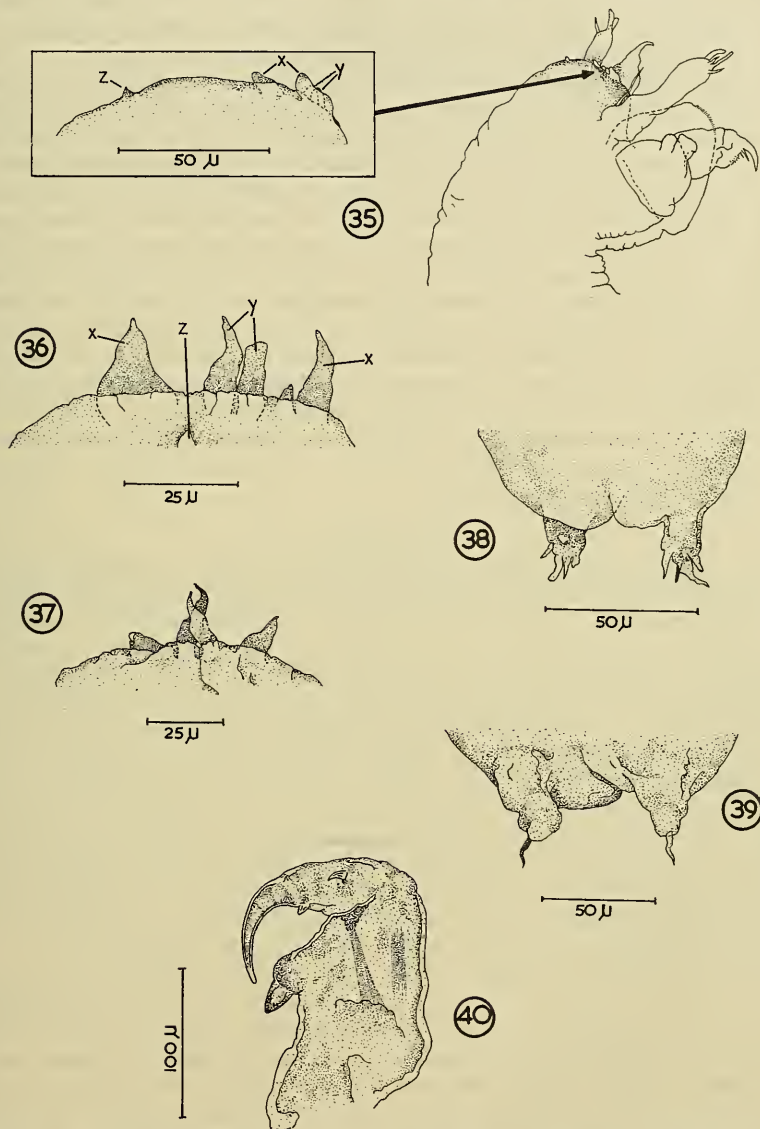
to the next developmental stage. This more advanced stage is shown in Figure 40. It has all the features of the adult appendage, but differs from it by the enormous elongation of the terminal claw of the subchela and the large size of the spine tipping the ventral tubercle.

The thoracopods (Figs 19–21, 23) could not be studied in detail, because of the shortage of material and poor stage of preservation. The only chalimus I available was, as mentioned above, ready to moult and the thoracopods of this specimen were no more than limp and empty cuticle with partly damaged setae hanging from the



Figs 25–34.—25. Chalimus I, 1st antenna, dorsal. 26. Chalimus I, 2nd antenna, medial. 27. Chalimus II, 2nd antenna, tip of endopod, medial. 28. Chalimus III, 2nd antenna, exopod, lateral. 29. Chalimus I, mandible, lateral. 30. Chalimus I, maxilla, exopod, ventro-lateral. 31. Chalimus I, 1st maxilliped and base of frontal filament. 32. Chalimus I, 2nd maxillipeds. (The cuticle of chalimus I pulled off the left appendage, showing that of next stage.) 33. Chalimus II, 2nd maxilliped liberated from the cuticle, to show the next stage. 34. Chalimus III, 2nd maxilliped, fully developed, lateral.

body of the animal. It could be seen (Fig. 23), however, that both pairs consisted of one-segmented sympods, each carrying also one-segmented endopods and exopods, provided with at least four setae. In chalimus II (Fig. 20), the legs become simple, one-segmented structures provided with a single seta each. In chalimus III the author



Figs 35-40.—35. Chalimus II, lateral view of anterior part (semi-diagrammatic). Arrow points to cephalic armature, enlarged in rectangular frame. 36. Chalimus III, cephalic armature, dorsal. 37. Chalimus IV, cephalic armature, dorsal. 38. Chalimus II, caudal furca, ventro-lateral. 39. Chalimus III, caudal furca, ventral. 40. Chalimus IV (or a later stage), 2nd maxilliped, lateral.

could find only one pair of thoracopods, which were no more than single setae with slightly inflated bases. No trace of the legs was found in the two specimens of chalimus IV examined.

The changes undergone by the caudal furca (Figs 24, 7, 4, 5, 6, 38, 39) are of considerable interest. Although the difficulties of study were here as great as with

the thoracopods, it could be seen that in chalimus I (Fig. 24) the anal furca consist of two blade-like segments, each equipped with six short though fairly robust setae. In chalimus II the blades are rather smaller and the number of setae decreases to four (Fig. 38), perhaps five. In chalimus III they become mere wart-like protuberances, tipped with a single seta each (Fig. 39). By the time the development has reached chalimus IV stage, the caudal furca have the appearance which persists until the adult stage. The changes, which occur then, are mentioned above.

Several noteworthy features were observed at the anterior end of the cephalothorax (Figs 35-37). As can be seen from Figure 35, the front end of the cephalothorax forms a bulbous "forehead", anterior to the mouth-cone. The apex of this forehead (with an arrow pointing to it in Fig. 35) is enlarged in the rectangular frame to show that it is equipped with five peculiar structures. Four of them are arranged in a transverse line (Fig. 35, *x*, *y*) and the fifth (*z*), a small denticle, is dorsal to them in the centre of the head. The line consists of two smaller, peg-like structures in the centre (*y*) and two larger, broad-based ones on the ends of the line and at some distance from the central pair. Figure 35 shows them in chalimus II. The author was unable to see similar structures in chalimus I. Figure 36 shows the same structures in chalimus III. At this stage the spines are larger and have sharper points than in the preceding stage. The central members (one of which has a broken tip in Fig. 36) are still slender, while the lateral members are broad-based and end in sharp points. In the examined specimen one of the lateral spines appears to have been broken, a part of it appearing as a small independent spine. In chalimus IV (Fig. 37) the cephalic armament persists without any changes.

DISCUSSION.

The first point made clear by the study of *Vanbenedenia chimaerae* is the similarity between its finer structural details and those of *V. kroyeri* (cf. Kabata and Bowman, 1961). These details are particularly evident in the structure of the antennae. As mentioned above, *V. chimaerae* has an inflated tip in its first antenna, which is unique to the genus. In discussing the first antenna of *V. kroyeri*, Kabata and Bowman stated that its apical armament included a powerful spine, which divided into two some way from its base. In the light of the present study, it seems certain that the structure should have been interpreted as the "central swelling", with two spines arising from its tip. Spines (4) and (6) were also present in *V. kroyeri*, though they were labelled (*b*) and (*d*) respectively. The second antennae of *V. chimaerae* also bear great resemblance to those of the other known species of the genus, particularly in the position of the rami and the armament of the endopod. Yet another similarity is provided by the mandible, which has characteristically small third tooth. In view of the diagnostic importance of the mandible (Kabata, 1963a), this point should not be overlooked when placing the present species in the genus *Vanbenedenia*.

The biological details, which can be inferred from the study of the specimens, also resemble those described for *V. kroyeri* (cf. Kabata, 1958, 1959) and are, apparently, unique among Lernaeopodidae. The author refers here to the fact that the young individuals of *Vanbenedenia* settle on the parent individuals and become attached to them by means of their frontal filaments, which in all other known genera are used for the attachment to the host directly. Of the 14 females examined, nine had either filaments or juvenile individuals attached to their cephalothoraces. The filaments ranged from 1 to 6 on one female, which suggests that this method of attachment is not an exception, but a normal occurrence in the genus. Three facts can account for this unusual method of settling of the free-swimming larvae; the host fish is not very common and normally does not occur in large schools; sometimes, therefore, it might be imperative for the newly-hatched parasite to gain hold of the host individual infested by the parasite's parent. Secondly, the area of the suitable attachment site appears to be limited. *V. kroyeri* has never been found attached to any other part of its host, except the dorsal fin or dorsal spine. The author (Kabata, 1959) recorded as many as seven parasites on one single spine. *V. chimaerae* appears to be limited to

the claspers of its host, the only known record showing as many as 50 parasites on one host fish. The parasites are rather large, which again means that they must be crowded and that the only way in which they can remain in contact with the host is by getting hold of the individuals of the parent generation, densely covering the available site.

The specimens, which the author examined in the course of this work, disclose the presence of at least four chalimus stages, with intervening moults, in the life history of *Vanbenedenia*. This fact provides a valuable addition to our imperfect knowledge of the life histories of Lernaeopodidae. Those members of the family whose life cycles have been studied so far show a tendency to the suppression of the chalimus stages, only the more primitive of them still retaining more than one chalimus stage in their development cycle. The tendency appears early in the family's history, with the primitive genera *Achtheres* and *Salmincola*. Wilson (1911) described the development of *Achtheres ambloplitis* Kellicott, 1880, which had a single chalimus stage. On the other hand, Zandt (1935) found as many as five chalimus stages in the development of *A. coregonorum* (Kessler, 1868). He presented evidence of the primitive character of this species. (It is of interest in this context that *A. ambloplitis* is among those more specialized species of its genus, which abandoned their original salmonid hosts to parasitize the more advanced percomorph fishes.) In the genus *Salmincola*, Friend (1941) described the one-chalimus cycle of *Salmincola salmonea* (Gissler, 1751). In contrast, *S. mattheyi* Dedie, 1940, has as many as five chalimus stages.

The caligid copepods, which are presumed to be close to the ancestral line of Lernaeopodidae, include sometimes even six chalimus stages (Lewis, 1963). Lernaeoceridae also have more than one (usually four) chalimus stages (Sproston, 1941; Kabata, 1958a). It appears, therefore, that Zandt's opinion on the primitive character of the multi-stage chalimus development in Lernaeopodidae was correct. *Vanbenedenia*, therefore, must be consigned among the more primitive members of the family.

In describing the male of *V. chimaerae*, Heegaard (1961) makes no mention of its mode of attachment. Apart from the definitely segmented trunk, his male shows no differences from the chalimus specimens examined by the author. The early investigators (Olsson, 1869) depicted the male of *Vanbenedenia kroyeri* as being attached by its frontal filament. Wilson (1915) did not question those descriptions; neither did the author himself in his earlier work (Kabata, 1958). In view of the present work, however, this opinion must be revised. As stated above, up to chalimus II no external differences between the sexes are observable. In chalimus III female the only distinguishing feature is the elongation of the first maxillipeds, which becomes very distinct in chalimus IV. Heegaard's description shows no such elongation. It is, therefore, possible that his description is the first record of the male of *Vanbenedenia*. It is certain that neither Olsson nor the author himself described an undoubtedly male specimen in their work.

The description of the development of the second maxilliped, shown in this paper, provides an excellent illustration of adaptive changes in the ontogeny of *Vanbenedenia*. This prehensile appendage develops progressively through the attached chalimus stages (Figs 32-34) to reach the peak at the time when the parasite is ready to relinquish the frontal filament and seek its permanent attachment to the host. At this stage, shown in Figure 40, the subchela of the second maxilliped is at its strongest, with the powerful claw, and the ventral tubercle is also strongly armed. It is obvious that the period transitional between the attachment by the frontal filament and that by the bulla requires this organ of prehension. Once the parasite becomes attached again, however, the need for prehension disappears and the second maxilliped undergoes regression, evident from Figures 17 and 18, illustrating this appendage in a young and a mature adult respectively.

The changes undergone by the caudal furca in the course of development of *V. chimaerae* throw some light on the fate of similar structures in other genera of

Lernaeopodidae. Kurz (1877) and Kabata (1964c) recorded the presence of small vestigial appendages near the centre of the posterior margin of the trunk in *Clavellisa emarginata* (Krøyer, 1837), while Gnanamuthu (1948) found them in his *C. dussumieriae*. Kurz suggested that these appendages represent the vestiges of thoracopods, a view opposed by Wilson (1915). It now seems probable that these structures, so similar in shape and position to the dwarfed caudal furca of the female *V. chimaerae*, are also homologous with them.

Describing the alleged male of *V. kroyeri*, the author (Kabata, 1958) noted the peculiar cephalic armament, never previously commented on, and suggested that this must be a juvenile feature. It is now clear that these structures are, indeed, juvenile, and that the sharp, spine-lamellae must be used in preparing the host tissues for the penetration of the parasite's bulla.

SUMMARY.

This paper gives a detailed description of the shape and appendages of *Vanbenedenia chimaerae* (Heegaard, 1962), originally described as a member of the genus *Tracheliastes*. The description includes the adult female and four developmental stages, referred to as chalimus I-IV. The concluding discussion asserts that morphological evidence places this parasite in the genus *Vanbenedenia* and that the genus should be considered as a primitive member of Lernaeopodidae. On the same basis inferences are made concerning the changing role of the maxillipeds and the fate of the caudal furca in the course of development of *Vanbenedenia*.

Acknowledgements.

The author wishes to acknowledge the assistance of Dr. Yaldwyn, Australian Museum, Sydney, in placing at the author's disposal specimens on which this work is based and in helping with the arrangements for its publication. The author is also grateful to Dr. Heegaard, the discoverer of *Vanbenedenia chimaerae*, for his comments and his very helpful attitude.

References.

- DEDIE, O., 1940.—Étude de *Salmincola mattheyi*, n. sp., copépode parasite de l'ombrie-chevalier (*Salmo salvelinus*, L.). *Rev. suisse Zool.*, 47: 1-63.
- FRIEND, G. F., 1941.—The life history and ecology of the salmon gill-maggot, *Salmincola salmonea* (L.). *Trans. roy. Soc. Edinb.*, 60: 503-541.
- GNANAMUTHU, C. P., 1948.—A new copepod parasite, *Clavellisa dussumieriae*, belonging to the subfamily Clavellinae, from the gills of a Madras fish. *Proc. zool. Soc. Lond.*, 117: 748-755.
- HEEGAARD, P., 1947.—Contribution to the phylogeny of the arthropods. *Copepoda. Spolia zool. Mus. Hauniensis*, 8: 1-280.
- , 1962.—Parasitic Copepoda from Australian waters. *Rec. Aust. Mus.*, 25 (9): 149-234.
- KABATA, Z., 1958.—*Vanbenedenia kroyeri* Malm., 1860: a rare parasitic copepod. *Ann. Mag. nat. Hist.* (13), 1: 331-335.
- , 1958a.—*Lernaeocera obtusa*, n. sp.; its biology and its effects on the haddock. *Mar. Res. Scot.*, 1958 (3): 1-26.
- , 1959 (1960).—*Vanbenedenia kroyeri* (Copepoda parasitica): Taxonomic review and other notes. *Ann. Mag. nat. Hist.* (13), 2: 731-735.
- , 1963.—*Clavella* (Copepoda) parasitic on British Gadidae: one species or several? *Crustaceana*, 5 (1): 64-74.
- , 1963a.—The second antenna in the taxonomy of Clavellinae (Copepoda, Lernaeopodidae). *Crustaceana*, 6 (1): 5-14.
- , 1964.—The morphology and the taxonomy of *Clavellodes pagelli* (Krøyer, 1863) (Copepoda: Lernaeopodidae). *Crustaceana*, 7 (2): 103-112.
- , 1964a.—Revision of the genus *Charopinus* Krøyer, 1863 (Copepoda: Lernaeopodidae). *Vidensk. Medd. dansk naturh. Foren. Kbh.* (in press).
- , 1964b.—Redescription of *Lernaeopoda centroscyllii* Hansen, 1923 (Copepoda: Lernaeopodidae). *J. Fish. Res. Bd Can.*, 21 (4): 681-689.
- , 1964c.—*Clavellisa emarginata* (Krøyer, 1837): Morphological study of a parasitic copepod. *Crustaceana*, 7 (1): 1-10.
- KABATA, Z., and BOWMAN, T. E., 1961.—Revision of *Tracheliastes grandis* Wilson, 1915 (Copepoda: Lernaeopodidae). *Crustaceana*, 3 (2): 120-126.
- KURZ, W., 1877.—Studien über die Familie der Lernaeopodiden. *Z. wiss. Zool.*, 29: 380-423.

- LEWIS, A. G., 1963.—Life history of the caligid copepod *Lepeophtheirus dissimulatus* Wilson, 1905 (Crustacea: Caligoida). *Pacif. Sci.*, 17 (2): 195-242.
- MONOD, T., and VLADYKOV, V., 1931.—Sur quelques copépodes parasites provenant de la Russie Sous-Carpathique (Tchécoslovaquie). *Ann. Parasit. hum. comp.*, 9: 202-224.
- OLSSON, P., 1869.—Prodromus faunae copepodorum parasitantium Scandinaviae. *Acta Univ. Lund.*, 1868: 1-49.
- WILSON, C. B., 1911.—North American parasitic copepods, Part 9: The Lernaeopodidae. Development of *Achtheres ambloplitis* Kellicott. *Proc. U.S. nat. Mus.*, 39: 189-226.
- , 1915.—North American parasitic copepods belonging to the Lernaeopodidae, with a revision of the entire family. *Proc. U.S. nat. Mus.*, 47: 565-729.
- ZANDT, F., 1935.—*Achtheres pseudobasanistes* n. syn. *Basanistes coregoni* (Neresheimer), die postembryonale Entwicklung und geographische Verbreitung eines Lernaeopodiden. *Zool. Jb. Anat.*, 60: 289-344.

